NEW GENUS OF FOSSIL FAGACEAE FROM THE SANTONIAN (LATE CRETACEOUS) OF CENTRAL GEORGIA, U.S.A.

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A new genus and species (Antiquacupula sulcata) is established for fossil staminate flowers, bisexual flowers, fruits, and cupules from the late Santonian (Late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, U.S.A. Together with Protofagacea, recently described from the same locality, these remains constitute the earliest fossil evidence of the Fagaceae sensu lato. Staminate flowers of the new genus are pedicellate, with six free tepals in two cycles of three, 12 free stamens, and a vestigial gynoecium with three styles. Bisexual flowers are epigynous and actinomorphic, with six free tepals in two whorls, 12 free stamens, and a syncarpous gynoecium with three styles. The ovary is trilocular, with two anatropous, apically pendulous ovules per locule. The styles are partially comate below, with trichomes around and between the style bases. Fruits are triangular in cross section, with nearly equal sides, and contain a single seed. Cupules comprising multiple series of bracts contain at least six fruits. The staminate and bisexual flowers both have slender, thin-walled nectary lobes between the filament bases and distinctive, multicellular glandular structures on the surface of the gynoecium. Pollen grains found in the anthers and on the surface of the flowers and fruits are small and tricolpate, with a finely perforate tectum. Comparison of these fossils to extant and fossil taxa clearly indicates a relationship to extant Fagaceae sensu lato, based on the presence of the cupule and flower and fruit morphology. The discovery of Antiquacupula, in addition to Protofagacea, indicates an early divergence of at least two lineages within the Fagaceae, both with cupules, by the Santonian. In addition, Antiquacupula shares several characters with extant rosids and hamamelids and may be a key taxon for clarifying the relationships among these groups as well as within the Fagaceae.

Introduction

The family Fagaceae sensu lato comprises nine genera and nearly a thousand extant species of monoecious trees and shrubs, including the beeches, oaks, and chestnuts (Heywood 1993; Linder and Crisp 1995). The group is predominantly distributed in the Northern Hemisphere, except for several genera that extend into the Southern Hemisphere, and Nothofagus, which is restricted to the Southern Hemisphere (Heywood 1993). The earliest evidence of Fagaceae sensu lato in the fossil record is documented by dispersed pollen similar to that produced by extant Nothofagus from the early Campanian and younger strata of southern Gondwana (Dettmann et al. 1990) and Protofagacea flowers and associated fruits and cupules from the late Santonian (previously thought to be early Campanian; see note added in proof) of southeastern North America (Herendeen et al. 1995). Early evidence of Fagaceae sensu stricto (i.e., excluding Nothofagus, which is now treated as a distinct family, the Nothofagaceae), is based on dispersed castaneoid pollen reported by Chmura (1973) from the Maastrichtian of California, but the affinities of these grains have been questioned because of the difficulty in distinguishing castaneoid pollen from that of other rosids (Crepet 1989; Crepet and Nixon 1989a). Megafoils assigned to the Fagaceae sensu stricto have been recovered from the early and middle Eocene of Tennessee (Crepet and Daghlian 1980; Jones and Dilcher 1988; Crepet and Nixon 1989a), the Eocene of Oregon (Manchester 1981, 1994), the Oligocene of Texas (Daghlian and Crepet 1983; Crepet and Nixon 1989b), and several other localities of early Tertiary age (see Herendeen et al. [1995] for a review).

The Fagaceae sensu lato are characterized by the presence of a cupule and have been divided tradition- ally among two or three subfamilies, the Fagioideae, Castaneoideae, and Quercoideae (Forman 1964, 1966a; Hutchinson 1967; Abbe 1974; Jones 1986; Heywood 1993). Recent cladistic analyses have shown the Fagaceae sensu lato to be paraphyletic, and they support recognition of the genus Nothofagus as a distinct family (the Nothofagaceae) separate from the Fagaceae sensu stricto. Analyses of morphological data by Nixon (1989) placed the Fagaceae sensu stricto in a basal position, with the Nothofagaceae resolved as sister group to the “higher” hamamelids (e.g., Betulaceae, Juglandaceae, Myricaceae). Recent cladistic analyses based on chloroplast DNA data also resolve the Fagaceae sensu lato as paraphyletic but support Nothofagaceae as basal, with Fagaceae sensu stricto resolved as sister group to the “higher” hamamelids (Chase et al. 1993; Manos et al. 1993; Martin and Dowd 1993; Manos and Steele 1997).

The structure and origin of the fagaceous cupule have been interpreted variously as fused inflorescence bracts, a de novo intercalary structure of the inflorescence axis, or a cladode-like structure formed from the outer (ultimate order) sterile axes of the dichasial inflorescence (Berridge 1914; Hjelmqvist 1948; Brett 1964; Forman 1966b; Abbe 1974; Endress 1977; MacDonald 1979; Fey 1981; Fey and Endress 1983; Kaul

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and Abbe 1984; Nixon 1989; Jenkins 1993; Herendeen et al. 1995). Whatever its morphological origin, given the paraphyly of the Fagaceae sensu lato, it is equally parsimonious to hypothesize independent origins of the cupule in Nothofagus and Fagaceae sensu stricto as it is to interpret the cupules as homologous structures that were lost in the “higher” hamamelids (Nixon 1989; Manos et al. 1993; Herendeen et al. 1995; Manos and Steele 1997). Evidence from the paleobotanical record of early, extinct members of the group may help to clarify relationships within the family and also to illuminate the evolutionary history of the cupule.

The recent description of Protofagaceae allonensis, a genus of fossil Fagaceae sensu lato from the Santonian of North America, by Herendeen et al. (1995) significantly extended the macrofossil record of the group. Staminate flowers and associated fruits and cupules of Protofagacea indicate a relationship to extant Fagaceae sensu lato, but the genus also shares some characters with Nothofagaceae. In this article we describe a new genus from the same locality as Protofagacea. The new fossil flowers, fruits, and cupules also exhibit features of the Fagaceae sensu lato but are morphologically distinct from P. allonensis. This material establishes the divergence of at least two lineages within Fagaceae sensu lato by the late Santonian.

**Material and Methods**

The fossil material described here was collected from the south pit (Allon quarry) of the Atlanta Sand and Supply Company (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W) in Gaillard, Georgia, ca. 9.5 km southeast of Roberta in Crawford County. The material was isolated from a carbonaceous clay lens that was exposed on the south face of the Allon quarry. The clay lens has been assigned to the Buffalo Creek Member of the Gaillard Formation (Huddleston and Hetrick 1991). Palynological analyses indicate that the Gaillard Formation is of late Santonian age (Christopher 1979 and personal communication 1998 [see note added in proof after Literature Cited]; Huddleston and Hetrick 1991). The Allon fossil flora contains a diverse assemblage of angiosperms, gymnosperms, ferns, and bryophytes, preserved as fusainized and lignitic mesofossils (Herendeen et al. 1995; Crane and Herendeen 1996; Keller et al. 1996; Magallón-Puebla et al. 1996; Konopka et al. 1997 and in press).

The material was prepared by dissolving bulk samples of clay in water and then washing through a series of sieves (finest mesh 125 μm). Isolated plant material was cleaned with HCl, followed by HF, and then thoroughly washed in water. The fossil material was air-dried and examined using a binocular stereomicroscope. Specimens were mounted on stubs, coated with gold, and examined with an Amray 1810 scanning electron microscope. After initial scanning, selected specimens were partially dissected to reveal internal anatomy and then recoated and scanned. All fossil specimens are deposited in the paleobotanical collections of the Department of Geology, Field Museum, Chicago (PP).

**Systematics**

**Family**—Fagaceae sensu lato

**Genus**—Antiquacupula Sims, Herendeen, and Crane, gen. nov.

**Type Species**—Antiquacupula sulcata Sims, Herendeen, and Crane, sp. nov.

**Generic Diagnosis**

Staminate flowers pedicellate, actinomorphic; tepals free, imbricate, in two cycles of three; stamens free in two cycles of six; stamen cycle opposite tepals develops first, followed by cycle alternate to tepals; anthers dorsifixed with longitudinal dehiscence slits; pollen grains small, tricolporate, tectum finely perforate; slender, thin-walled structures (interpreted as nectary lobes) alternate with stamens; vestigial gynoecium with three short style lobes, ovary absent; numerous small, multicellular, glandular structures scattered on the surface of style bases; gynoecium and stamen filaments surrounded by simple trichomes.

Bisexual flowers epigynous, actinomorphic; tepals free, imbricate, in two cycles of three; stamens free, in two cycles of six; anthers dorsifixed with longitudinal dehiscence slits; pollen grains small, tricolporate, tectum finely perforate; slender, thin-walled structures located between each filament base (interpreted as nectary lobes); gynoecium tricarpellate, ovary inferior, trilocular, placation apical, ovules anatropous, two per locule; styles three, partially connate at the base; surface of ovary covered with simple trichomes; numerous small, multicellular glandular structures scattered on the surface of style bases.

Cupules comprise multiple series of bracts and contain at least six closely aggregated bisexual flowers/ fruits. Fruits triangular in cross section with sides of approximately equal length; outer tepals located on the corners of the fruits, inner tepals centered on each face; associated pollen grains small, tricolporate, tectum finely perforate; slender, thin-walled structures (interpreted as nectary lobes) located between filament

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**Figs. 1–8** Staminate flowers of Antiquacupula sulcata. Fig. 1, Lateral view of staminate flower bud with tips of stamens visible; PP44771; × 70. Fig. 2, Lateral view of mature staminate flower with pedicel and attached anthers; PP44767; × 40. Fig. 3, Tepal, showing acute apex and trichomes on margins; PP44771; × 135. Fig. 4, Staminate flower, showing anthers and styles; PP44768; × 75. Fig. 5, Staminate flower, showing six tepals in two cycles, 12 filaments opposite and alternate to the tepals, elongated nectary lobes between stamen bases, and gynoecium of three fused style bases; PP44769; × 30. Fig. 6, Detail of staminate flower, showing filaments with trichomes, swollen filament bases, and elongated nectaries between the stamens. Arrows indicate two of the nectaries. PP44770; × 60. Figs. 7, 8. Partially dissected bud of staminate flower; PP44771. Fig. 7, Lateral view of partially dissected bud, showing stamens of two different cycles; the cycle opposite the tepals has anthers placed higher and more enlarged filament bases; × 70. Fig. 8, Detail of stamen bases, showing difference in swelling of the filament bases between the two cycles of stamens and an elongated nectary (arrow) between the filament bases; × 280.
Figs. 9–17 Staminate flowers of *Antiquacupula sulcata*. Fig. 9, Filament from staminate flower, showing enlarged filament base and apical hook to dorsifixed anther; PP44771; $\times$ 150. Fig. 10, Ventral side of anther from staminate flower, with apical projection; PP44768; $\times$ 350. Fig. 11, Mature anther (isolated) with open pollen sacs, showing smooth inner surface of thecae and apical projection; PP44756; $\times$ 250. Fig. 12, Dorsal side of immature anther from staminate flower bud, showing point of attachment of filament and partial separation of thecae; PP44771; $\times$ 350. Fig. 13, Pollen of *A. sulcata* from staminate flower; tricolporate grains with finely perforate tectum; PP44767; $\times$ 2800. Fig. 14, Enlargement of dissected staminate flower, showing three styles, fused at the base, and trichomes around and between the base of the styles; PP44793; $\times$ 87. Fig. 15, Partially dissected staminate flower bud, showing gynoecium and two cycles of anthers; PP44768; $\times$ 75. Fig. 16, Detail of gynoecium surface, showing multiple small glands scattered on the surface; PP44768; $\times$ 200. Fig. 17, Detail of gland on surface of gynoecium; PP44769; $\times$ 800.
Figs. 18–26  Fruits of *Antiquacupula sulcata*. Fig. 18, Lateral view of fruit showing fused stylar base and moderate ribbing of fruit wall; PP44761; × 15. Fig. 19, Lateral view of fruit with attached tepal and well-developed ribbing of fruit wall; PP44760; × 15. Fig. 20, Apical view of mature fruit showing attached filaments and styles united at the base; PP44761; × 30. Figs. 21, 22, Immature fruit; PP44765. Fig. 21, Apical view of fruit with trichomes, stamens with attached anthers, swollen filament bases, and nectary lobes between filament bases; × 75. Fig. 22, Detail showing trichomes, broken tepal base, swollen filament bases and nectary lobes; × 100. Fig. 23, Detail of swollen filament base from fruit preserved in cupule; PP44751, holotype; × 225. Fig. 24, Oblique view of abraded, mature fruit; PP44577; × 25. Fig. 25, Oblique view of abraded, mature fruit, showing partially preserved style bases and nectary lobes; PP44594; × 20. Fig. 26, Detail of apex of an abraded fruit, showing characteristic preservation of tepals, swollen stamen bases, nectary lobes, and styles; PP44594; × 37.
bases; numerous small, multicellular glandular structures dispersed on the surface of style bases; mature fruits contain a single seed.

Species—*Antiquacupula sulcata* Sims, Herendeen, and Crane, sp. nov. (Figs. 1–50)

**Specific Diagnosis**

*Staminate flower.* As for the genus, with the following additions: staminate flowers ca. 2–3 mm in diameter; tepals ca. 1 mm long, ca. 0.25 mm wide at the base, tapering to an acute apex; simple trichomes on margins, tip, and exterior surface of tepals; anthers ca. 0.1–0.3 mm long with distinctive knoblike apical projection; filaments with swollen bases at maturity; pollen grains small (polar axis ca. 12–13 μm long, diameter ca. 8–11 μm); slender nectary lobes located between each filament base, ca. 0.1 mm in diameter, ca. 0.4 mm long; multicellular glandular structures on surface of style bases, ca. 0.4–0.6 mm in diameter.

*Bisexual flower.* As for the genus, with the follow-
Figs. 44–50 Cupules of *Antiquacupula sulcata*. Figs. 44–47. Immature cupule with three fruits; PP44753. Figs. 44, 45, Lateral view from both sides, illustrating four primary lobes and arrangement of bracts; × 30. Fig. 46, Apical view of lateral fruit. Fig. 47, Apical view of central fruit; × 75. Figs. 48–50, Partial cupule with one mature fruit; PP44752; all × 25. Fig. 48, Lateral view of cupule illustrating bract structure. Fig. 49, Apical view showing triangular fruit outline (cf. figs. 20, 24, 25). Fig. 50, Oblique view of cupule, illustrating bract structure.
ing additions: simple trichomes on margins, tip, and abaxial surface of tepals; anthers ca. 0.1–0.3 mm long with distinctive knoblike apical projection; pollen grains small (polar axis ca. 12–13 μm long, diameter ca. 8–11 μm); filament bases swollen at maturity; slender nectary lobes located between each filament base, ca. 0.1 mm in diameter, ca. 0.4 mm long; multicellular glandular structures on surface of style bases, ca. 0.4–0.7 mm in diameter.

**Fruit.** As for the genus, with the following additions: fruits ca. 2–4 mm in length, ca. 2–3 mm in maximum width; longitudinally ribbed fruit walls, with three to five ribs per side; filaments have swollen bases at maturity; slender nectary lobes located between each filament base, ca. 0.1 mm in diameter and ca. 0.4 mm long; multicellular glandular structures on surface of style bases, ca. 0.4–0.7 mm in diameter.

**Holotype**

PP44751 (figs. 23, 29, 39–43).

**Additional Material (Paratypes)**

**Staminate flowers.** PP44766, PP44767 (figs. 2, 13), PP44768 (figs. 4, 10, 15, 16), PP44769 (figs. 5, 17), PP44770 (fig. 6), PP44771 (figs. 1, 3, 7–9, 12), PP44793 (fig. 14).

**Cupules.** PP44752 (figs. 48–50), PP44753 (figs. 27, 33, 34, 44–47).

**Isolated fruits.** PP44594 (figs. 25, 26), PP44757 (fig. 24), PP44758, PP44759, PP44760 (fig. 19), PP44761 (figs. 18, 20, 30–32, 35), PP44762 (figs. 36–38), PP44763, PP44764, PP44765 (figs. 21, 22, 28), PP44766, PP44821, PP44822.

**Isolated anthers.** PP44755, PP44756 (fig. 11).

**Type Locality**

South pit of the Atlanta Sand and Supply Company, Gaillard, Georgia, approximately 9.5 km southeast of Roberta in Crawford County (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W) (Herendeen et al. 1995).

**Stratigraphic Position**

Buffalo Creek Member, Gaillard Formation.

**Age**

Late Santonian (Late Cretaceous).

**Description and Remarks**

The new species is established for staminate flowers (figs. 1–17), bisexual flowers (figs. 18–23), fruits (figs. 24–38), and cupules (figs. 39–50). The floral organization of the staminate and bisexual flowers is summarized in figure 51.

**Staminate flower.** Staminate flowers are pedicellate and actinomorphic (figs. 1, 2, 5). The perianth consists of six free, imbricate tepals in two whorls of three (figs. 1, 4, 5). Tepals are ca. 0.9 mm long and ca. 0.25 mm wide at the base and taper to an acute apex, with numerous simple trichomes on the margins and abaxial surface (fig. 3).

The androecium is composed of 12 free stamens in two cycles of six (figs. 5–8). Between adjacent stamen bases is a slender, elongated, thin-walled structure (ca. 0.1 mm in diameter and ca. 0.4 mm long) that we interpret as a nectary lobe (figs. 5, 6, 8). Stamens consist of a filament and dorsifixed anther (figs. 9–12). Filaments are thin (ca. 0.1 mm in diameter), with simple trichomes (figs. 6, 9), and at maturity extend beyond the tips of the tepals (fig. 2). Mature stamens have distinctive, swollen filament bases (figs. 7–9). Anthers are ca. 0.2 mm long and dehisce by simple longitudinal slits (figs. 10–12). The anthers have a wrinkled epidermal surface but are more or less smooth internally (within the theca) (figs. 10, 11). The anthers are dorsifixed and the thecae are connected for approximately two-thirds the length of the anther (figs. 10, 12). The connective is developed into a distinctive, knoblike apical projection, ca. 0.4 mm wide at the base and ca. 0.4 mm long (fig. 11). The cycle of stamens opposite the tepals develops first, followed by the cycle alternate to the tepals, as evidenced by the relative maturity of anthers (figs. 7, 10, 12, 15) and the differing degree of enlargement of the filament bases (figs. 7, 8). In the bud, anthers of the cycle opposite the tepals are positioned above those of the alternate cycle.

![Fig. 51 Schematic diagrams of fossil staminate flower (A) and bisexual flower (B) summarizing the structural organization of Antiquacupula sulcata.](image-url)
(figs. 7, 15). Pollen grains are tricolporate and small (polar axis ca. 12–13 μm long, diameter ca. 9–11 μm), with a finely perforate tectum (fig. 13).

The flowers have a vestigial, tricarpellate gynoeceum with three styles that are partially connate at the base. The ovary is absent. The free portion of each style is terete, tapering distally (fig. 14). A stigmatic surface is not apparent, but the majority of specimens are preserved with the gynoecium broken below the level at which the styles diverge. None of the specimens shows evidence of an ovary. There are simple trichomes in the center of the flower, around and between the style bases (fig. 14). Numerous small, multicellular, glandular structures (diameter ca. 0.6 mm) are scattered on the surface of the style bases (figs. 16, 17).

**Bisexual flower.** The bisexual flowers are epigynous and actinomorphic (figs. 18–21). The perianth, which is abraded in many specimens, is comprised of six free, imbricate tepals in two whorls of three (figs. 19–21, 46, 47). Tepals are ca. 0.9 mm long and ca. 0.25 mm wide at the base and taper to an acute apex (figs. 19, 46, 47).

The androecium consists of 12 free stamens in two cycles of six (figs. 20, 21). Between adjacent stamen bases is a slender, thin-walled structure (ca. 0.1 mm in diameter and ca. 0.4 mm long) that we interpret as a nectary lobe (figs. 21, 22). Stamens consist of thin filaments and dorsifixed anthers (figs. 20, 27–29). Filaments are thin (ca. 0.1 mm in diameter), with simple trichomes (figs. 20–22). Mature stamens have distinctive, swollen filament bases (figs. 23, 26). Anthers are ca. 0.2 mm long and dehisce by simple longitudinal slits. The anthers have a wrinkled epidermal surface pattern and are more or less smooth internally (within the theca) (figs. 27–29). Anthers are dorsifixed and the thecae are connected for approximately two-thirds the length of the anther (figs. 27, 28). The connective is developed into a distinctive, knoblike apical projection, ca. 0.4 mm wide at the base and ca. 0.4 mm long (fig. 27). Pollen grains are tricolporate and small (polar axis ca. 12–13 μm long, diameter ca. 8–11 μm), with a finely perforate tectum (figs. 30–32).

The gynoecium is tricarpellate, with three styles that are partially connate at the base. The free portion of the styles is terete, tapering toward the tip (figs. 18, 21, 33, 34). A stigmatic surface is not apparent, but the majority of specimens are preserved with the gynoecium broken below the level at which the styles become free. There are numerous simple trichomes on the surface around and between the styles (figs. 21–23). Numerous small, multicellular, glandular structures (diameter ca. 0.6 mm) are scattered on the surface of the style bases (figs. 34, 35). The ovary is trilocular, with two anatropous, pendulous ovules per locule (figs. 36–38). There is no evidence of locular trichomes.

**Fruit.** Mature fruits are ca. 3.2 mm high (not including perianth, which is usually broken or abraded), with longitudinally ribbed fruit walls (three to five ribs per side). The prominence of ribbing differs between specimens and is not correlated with the size and degree of maturity of the fruit/seed (based on ovule/seed development) (figs. 18, 19, 24, 25). In cross section, the fruits are triangular, with nearly equal sides (ca. 1–2 mm in width on each face) (figs. 20, 49). The perianth is comprised of six free tepals in two whorls of three but is abraded in most specimens (figs. 21, 24–26). Tepals of the outer whorl are located at the corners of the fruit and tepals of the inner whorl are centered on each face (figs. 20–26). Tepals taper to an acute apex. The apex of the fruit is pyramidal (figs. 18, 24). There are simple trichomes around and between the style bases (figs. 21–23). Numerous small, multicellular, glandular structures (diameter ca. 0.6 mm) are scattered on the surface of the style bases of the fruits (fig. 35). Immature fruits have a spongy mesocarp surrounding the locules and a central vascular bundle running from the base to apex of the fruit (fig. 37). Mature fruits contain a single seed, which fills the entire inner cavity of the fruit.

**Cupule.** Bisexual flowers and fruits are borne in cupules (figs. 39–50). Three cupule specimens, each containing fruits at different stages of maturity, have been recovered from the same samples that yielded the staminate flowers, isolated fruits, and isolated anthers. The degree of maturity of the cupules and fruits is inferred from their relative size and the developmental stage of the fruits.

Cupules of *Antiquacupula sulcata* are four-lobed and pedunculate. One cupule specimen (PP44751) contains six closely aggregated immature fruits, each subtended by multiple series of bracts (figs. 39–43). The cupule is 5.0 mm from base to apex, 2.0 mm in maximum width, and 3.5 mm in maximum breadth. Outermost in the cupule are four large bracts, each subtending one of the four primary lobes of the cupule (figs. 39, 40). Internal to this series is a second series of four large bracts with the same positioning (figs. 39, 40). Adaxial to each of these are one to two series of two smaller, narrower bracts. The most complete cupule specimen (figs. 39–43) contains at least six fruits, and the poorly preserved bases of additional fruits also may be present (fig. 41). In this specimen, the central immature fruit in the cupule is tetracarpellate, but details of the androecium and tepal structure are not clear (fig. 43). The remaining immature fruits in the cupule are tricarpellate, and of the numerous isolated fruits studied, none are tetracarpellate. One tricarpellate fruit is preserved with elongate filaments and intact and nearly mature anthers (fig. 42).

The second cupule specimen (PP44753) contains three tricarpellate fruits subtended by two series of bracts (figs. 44–47). The fruits are arranged in a row, with the central fruit raised slightly above the laterals. The cupule is 2.4 mm from base to apex. In the transverse plane, the cupule apex is 1.1 mm in maximum width and 2.6 mm in maximum breadth. The specimen is abraded at the base and it is possible that originally there were further series of bracts external to those
preserved. Outermost in the cupule is a series of four large bracts, each of which subtends one of the four primary lobes of the cupule (figs. 44, 45). Internal to each is a second series of two smaller, narrower bracts. The fruits contained within the cupule are all triangular, tricarpellate, and of approximately equal size. The fruits are identical in structure to those found isolated (figs. 33, 46, 47). One lateral fruit was preserved with an immature anther with the characteristic apical projection. Pollen grains are poorly preserved but tricolporate and 8–11 μm in diameter. The sides of the cupule are slightly concave, flaring outward at the level of the fruit apices. In contrast, in the presumed more mature specimen (figs. 48–50), the cupule is more rounded at the base, suggesting that as the developing fruits enlarge, the cupule broadens at the base.

The third cupule (PP44752), interpreted as the most mature, is incomplete and consists of two cupule lobes subtending a single, mature tricarpellate fruit (figs. 48–50). This cupule is broken on one side. Each cupule lobe is composed of four series of bracts (fig. 50). The cupule is 2 mm from base to apex and at the apex is 2 mm along the broken edge and 1.5 mm wide from the center of the broken edge to outer bracts at the point of maximum diameter. The outermost structure in the cupule fragment is a single continuous bract (fig. 48). Internal to this is a series of two large bracts, each subtending a side of the fruit. Adaxial to each of these are two bracts, which in turn subtend a series of two smaller, narrower bracts (fig. 50). Numerous simple trichomes are present on the abaxial surfaces of the bracts. The shape and size of the fruit (ca. 1–2 mm long on each face) and the size of the cupule indicate that this is a relatively mature specimen. In addition, the shape of the cupule fragment is strongly convex and relatively wider at the base.

Association of Fruits, Flowers, and Cupules

We interpret the fossil staminate flowers (figs. 1–17), bisexual flowers and fruits (figs. 18–38), cupules (figs. 39–50), and isolated anthers (fig. 11) as parts of the same plant species for the following reasons: (i) staminate flowers have the same structural organization as the bisexual flowers and fruits, except for the presence of a vestigial rather than functional gynoecium (figs. 5, 20, 51); (ii) staminate flowers, isolated fruits, and fruits preserved within cupules show similar swollen filament bases at maturity (figs. 8, 23, 26); (iii) both staminate and bisexual flowers have comparable slender, thin-walled nectary lobes between the stamen bases (figs. 6, 22); (iv) both staminate and bisexual flowers have a distinctive apical projection on anthers (figs. 11, 27); (v) pollen identical to that produced by the staminate flowers occurs on the apical portions of eight fruit specimens and in high concentrations on a single fruit specimen preserved with intact filaments (figs. 13, 30–32); (vi) distinctive multicellular glandular structures are scattered on the surface of the gynoecium of the staminate flowers, bisexual flowers, and fruits (figs. 16, 17, 35); (vii) cupule specimens have bisexual flowers/fruits preserved in situ that are morphologically identical to isolated fruits (figs. 20, 42, 49).

Discussion

Systematic Relationships of Antiquacupula

The quality of preservation of Antiquacupula and the availability of staminate, bisexual flowers, fruits, cupules, and isolated anthers provide numerous characters for evaluating the systematic relationships of the reconstructed plant (table 1). Under traditional interpretations, the presence of a cupule, trimerous flowers, and an inferior, trilocular ovary with two apically attached, pendulous, anatropous ovules per locule are all characters of extant Fagaceae sensu lato. The presence of a cupule is widely considered the most diagnostic feature of Fagaceae sensu lato. Together these features support the relationship of Antiquacupula to the Fagaceae sensu lato. However, at a more detailed level, the data are insufficient for confident assignment to a particular taxon within Fagaceae sensu lato. Antiquacupula shares characters with both Nothofagaceae and Fagaceae sensu stricto (table 1), as well as with some families of Rosidae. In particular, Antiquacupula and Fagaceae sensu stricto both have dorsifixed anthers (vs. basifixed anthers in Nothofagus) and two cycles of tepals (vs. one cycle in Nothofagus). However, like Nothofagus and several species of Quercus (P. S. Manos, personal communication), Antiquacupula has a pronounced extension of the connective (lacking in most Fagaceae sensu stricto) and, as far as can be determined from the material available, also has glabrous fruit locules (Fagaceae sensu stricto have locular trichomes). Antiquacupula differs from both Fagaceae sensu stricto and Nothofagaceae in the possession of some likely plesiomorphic features such as well-developed nectary lobes and multicellular glands on the ovary surface (absent in extant Fagaceae but present in some rosiids) and in the structure of the pollen tectum (perforate) (table 1).

Evaluating the relationships of Antiquacupula is further complicated by uncertainties in the relationships among extant Fagaceae. Recent cladistic analyses of morphological and/or molecular data have shown the Fagaceae sensu lato to be paraphyletic, and Nothofagus has been recognized as a separate family from Fagaceae sensu stricto (Nixon 1989; Chase et al. 1993; Manos et al. 1993; Manos 1997; Manos and Steele 1997). Under this interpretation, the presence of a cupule is no longer an unambiguous synapomorphy for the group (fig. 52), and thus the presence of a cupule in the fossil taxon supports a relationship to this fagaceous grade, but it does not help to resolve relationships with respect to Fagaceae sensu stricto versus Nothofagaceae. Therefore, the approach we take here is to assign Antiquacupula to Fagaceae sensu lato, with the recognition that future work may require that this assignment be revised as relationships among extant Fagaceae and Nothofagaceae become clearer.
There has been considerable debate over the evolutionary origin of the fagaceous cupule (Berridge 1914; Hjelmqvist 1948; Brett 1964; Forman 1966b; Abbe 1974; Endress 1977; MacDonald 1979; Fey 1981; Fey and Endress 1983; Kaul and Abbe 1984; Nixon 1989; Jenkins 1993; Herendeen et al. 1995) and the question is further complicated by the possibility that the structure evolved twice, or evolved once and has been lost in a number of groups related to the Fagaceae (fig. 52). Nixon (1989) supported the interpretation of nonhomology among the cupules of Nothofagaceae and Fagaceae sensu stricto with observations that cupules in Fagaceae sensu stricto consistently have valves numbering one more than the total number of flowers \((n + 1)\), while the cupules of Nothofagus have more variation in the flower-to-valve ratio. However, recent work (Manos 1997) shows that the species of Nothofagus with cupules that deviate from the \(n + 1\) plan are derived within the genus.

The cupule of Antiquacupula (four-lobed and bearing at least six bisexual flowers, with the lateral flowers subtended by multiple [possibly four] series of bracts) appears to violate the \(n + 1\) rule. In contrast, Protofagacea, with three pistillate flowers per four-lobed cupule, clearly conforms to the \(n + 1\) rule and thus is consistent in cupule structure with Fagaceae sensu stricto. Detailed morphological study of cupules in extinct and extant Fagaceae, coupled with clarification of relationships among extant hamamelids, selected lower rosids, Protofagacea, and Antiquacupula will be crucial to further clarification of homologies of the fagaceous cupule and the evolutionary history of the Fagaceae.

Comparison of Antiquacupula and Protofagacea

Antiquacupula shares several morphological features with Protofagacea, which was described from the same fossil assemblage and was also assigned to the Fagaceae sensu lato (Herendeen et al. 1995) (table 1). The two taxa are similar in floral structure, with six tepals in two cycles of three, and 12 stamens in two cycles of six (typical of Fagaceae sensu stricto). In addition, both have dorsiﬁxed anthers with thecae that are separated in the apical portion of the anther, tricolporate pollen, and unisexual staminate flowers. However, the flower, fruit, and cupule morphology of Antiquacupula and Protofagacea differ in several significant features. The swollen stamen bases, the knoblike extension of the connective, multicellular glands on the gynoecium, and the presence of nectary lobes are all highly distinctive characteristics of Antiquacupula flowers that are absent in Protofagacea. In addition, the two genera differ in pollen size and exine sculpture and in the shape of the fruits (Antiquacupula fruits have equal-width sides; Protofagacea fruits have unequal-width sides).

The pedicellate staminate flowers of Antiquacupula differ from the sessile, staminate flowers of Protofagacea, as well as from those of most extant Fagaceae sensu lato, which are all sessile except for Fagus and Nothofagus (Heywood 1993) (table 1). The pistillode is also relatively well developed in the staminate flowers of Antiquacupula (although the ovary itself is very

<table>
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<th>Table 1</th>
<th>Comparison of Morphological Features in Nothofagaceae, Fagaceae sensu stricto, (Subfamilies Fagioideae and Castaneoideae), Protofagacea, and Antiquacupula</th>
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</thead>
<tbody>
<tr>
<td>Taxon</td>
<td>Number of tepal cycles</td>
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<tr>
<td>Nothofagaceae</td>
<td>3-9</td>
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<td>Fagaceae</td>
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<tr>
<td>Antiquacupula</td>
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Note: The subfamily Fagioideae contains the genera Fagus, Quercus, Trigonobalanus, Guazuma, and Ceylonarcturus. The subfamily Castaneoideae contains the genera Chrysobalanus, Castanea, Catanus, and Lithocarpus. Staminate flowers are not sufficiently well preserved to determine if pistillode flowers were fertile or staminodial.
poorly developed), compared to the greatly reduced gynoecium of *Protofagacea*. This is consistent with the interpretation that *Antiquacupula* retains more of the plesiomorphic characteristics of bisexual flowers and entomophily (e.g., nectary lobes) encountered in many rosid taxa. The apparent absence of trichomes in the fruit locule of *Antiquacupula* (not unequivocally confirmed because of poor preservation) may be another significant difference from other members of the Fagaceae *sensu stricto* and *Protofagacea*.

The cupules associated with *Protofagacea* by Herendeen et al. (1995) closely resemble those containing fruits of *Antiquacupula* in overall shape and in being four-valved (cf. figs. 39–50 here with figs. 49–57 of Herendeen et al. [1995]). However, there are several key features in which these cupules differ. The cupules of *Antiquacupula* contain as many as six fruits, and all of the numerous isolated specimens are tricarpellate, as are all of the fruits preserved in cupules (except for one tetracarpellate central fruit in the immature six-fruited cupule). In contrast, mature cupules of *Protofagacea* bear three abscission scars: two laterals that are triangular in shape and a central oblong scar that is thought to have been formed by a lenticular, bicarpellate fruit. Although none of the *Protofagacea* cupules studied thus far is preserved with fruits in situ, both tricarpellate (triangular) and bicarpellate (lenticular) fruits of *Protofagacea* have been recovered as isolated specimens, supporting the association made by Herendeen et al. (1995) on the basis of the size and shape of the scars.

Evolutionary Implications of *Antiquacupula*

The discovery of *Antiquacupula sulcata* from the same fossil assemblage that yielded *Protofagacea albonensis* (Herendeen et al. 1995) establishes the divergence of at least two lineages of Fagaceae *sensu lato* by the Santonian (Late Cretaceous). Previously, the presence of castaneoid and trigonobalanoid (subfamily Fagoideae) infructescences and fruits from the Paleocene of Tennessee has been used to indicate the divergence of the two subfamilies of Fagaceae (castaneoids and fagoids) by the early Tertiary or Late Cretaceous (Crepet and Nixon 1989a). The discovery of *Antiquacupula* provides evidence of a Cretaceous diversity in the family and supports the dispersed pollen record documenting the presence of Fagaceae *sensu lato* by at least the Campanian (*Nothofagus*-like pollen reported by Dettman et al. 1990). Current phylogenetic hypotheses indicate that the Fagaceae are nested within the largely insect-pollinated rosids (fig. 52) but, because they are also closely related to several predominantly wind-pollinated groups of extant “higher” hamamelids, the family can be thought of as somewhat intermediate in a trend from entomophilous plants with tricolporate pollen to anemophilous plants with triporate and stephanoporate pollen (Nixon 1989). *Antiquacupula* and *Protofagacea* contribute new data on some of the early Fagaceae that may have been involved in this transition. The presence of nectary lobes in *Antiquacupula* is an especially interesting feature that, as far as we know, does not occur in any extant Fagaceae. As further information accumulates on early Fagaceae, comparisons with fossil flowers of the Normapolles complex, as well as with extant and fossil rosids, should be important in clarifying patterns of morphological evolution in this important group of flowering plants.

Acknowledgments

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Literature Cited


Note Added in Proof

The age of the Allon deposit was recently reinterpreted as late Santonian based on palynological evidence (R. A. Christopher, Clemson University, written communication, 1998). Although a palynologic zonation for the Upper Cretaceous of the southeastern Coastal Plain Province has yet to be published, Christopher examined terrestrial palynomorphs from the Allon locality and considers the sediments to be biostratigraphically equivalent with marine units that have been assigned a late Santonian age on the basis of calcareous nanofossils (i.e., equivalent to the lower part of calcareous nanofossil zone CC17, which Burnett [1996] considers late Santonian). The age of the Allon locality was previously cited as early Campanian based on a less precise understanding of the biostratigraphy (Herendeen et al. 1995; Crane and Herendeen 1996; Keller et al. 1996; Magallón-Puebla et al. 1996; Konopka et al. 1997).